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GILL DIMENSIONS IN PELAGIC ELASMOBRANCH FISHES

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Abstract

The warm-bodied great white shark, Atlantic shortfin mako, and common thresher shark exhibit larger total gill surface areas than do ectothermic blue sharks, sandbar sharks, dusky sharks, or scalloped hammerhead sharks. The means by which the three former species have achieved this greater gill surface area differ. Total filament length per given body size in the great white shark is greater than in any other species of elasmobranch examined. In contrast, the Atlantic shortfin mako and common thresher sharks appear to rely upon larger secondary lamellae area as a means of increasing total gill surface area. None of the three species exhibit spacing of secondary lamellae which differ significantly from the arrangements found in the ectothermic species of elasmobranchs. Larger gill surface areas per unit body weight allow for greater volumes of water to be used effectively in the transference of oxygen to the blood, thereby increasing the total amounts of oxygen available to support the high energy physiology of the warm-bodied species.

Introduction

Measurements of gill dimensions for the purpose of estimating total area of respiratory surface have been made for a number of species of teleosts (notably Gray, 1954; Hughes, 1966; Muir, 1969; Muir and Hughes, 1969; Hughes and Morgan, 1973). Corresponding studies on elasmobranchs are fewer, and are confined to small and/or more sedentary species (Boylan and Lockwood, 1962; Hughes and Wright, 1970; Hughes, 1972; Hughes and Morgan, 1973). In addition, very few of the gill studies to date (teleosts or elasmobranchs) have utilized sufficient numbers of individuals within a species to investigate the relationships between surface area and body weight. Lamnid sharks are warm-bodied (Carey and Teal, 1969a; Carey *et al.,* 1982) in a manner similar to tunas (Carey, 1969b; Carey *et al.,* 1971). The latter group possesses unusually large gill surface areas (Muir and Hughes, 1969), approaching respiratory area estimates of mammalian lungs (Tota, 1978). No attempts have been made to estimate gill surface areas for any of the lamnid sharks, nor measurements conducted to provide estimates of gill areas in active, pelagic species of shark which have not developed an endothermic metabolism. The present report gives measurements of gill dimensions and estimates of total gill surface area in two warm-bodied elasmobranchs, the great white shark (*Carcharodon carcharias*) and Atlantic shortfin mako (*Isurus oxyrinchus*); one suspected endotherm (Carey, 1982), the common thresher shark (*Alopias vulpinus*); and four species of active, pelagic, ectothermic sharks: the

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sandbar (*Carcharhinus plumbeus*), dusky (*C. obscurus*), blue (*Prionace glauca*), and scalloped hammerhead shark (*Sphyrna lewini*).

Materials and Methods

Gills were removed from freshly killed specimens of known length and weight and preserved in 10 percent buffered formalin. Total gill surface areas were estimated by the methods of Hughes (1966) and Muir and Hughes (1969):

$$\text{Total Surface Area (TSA)} = 2(L \times d)bl$$

Where L is the total length of all filaments (mm), d is the number of secondary lamellae per mm on one side of a filament, and bl is the surface area (mm^2) of both sides of an average secondary lamella. For each gill arch, the total number of filaments was counted, and the total filament length determined using a dial caliper. The surface area of an individual secondary lamella was measured by tracing its image from a Nikon microscope equipped with a camera lucida microprojection head and subsequently tracing that drawing with a Lasico Model N-30 Planimeter.

Secondary lamellae were sampled from every twentieth filament on the first holobranch. Counts of secondary lamellae were made over the length of these filaments with a microscope equipped with an ocular micrometer (minimum of six counts of lamellae falling within the field of the micrometer from the base to the tip of the filament). A minimum of three lamellae from three different levels on the filament were carefully removed for determination of surface area: one from the base of the filament, one from the middle, and one from the tip. Secondary lamellae were removed with a scalpel and/or razor blade.

The first holobranch was examined in every specimen and complete gill sets were examined in: 4 *Alopias vulpinus;* 6 *Carcharodon carcharias;* 4 *Isurus oxyrinchus;* 4 *Carcharhinus plumbeus;* 3 *Carcharhinus obscurus;* 4 *Prionace glauca;* and 2 *Sphyrna lewini*. From these complete sets, the mean percentage of total filament length attributable to the first holobranch was calculated. This value was used to estimate total filament lengths for those animals of the same species from which only the first holobranch had been obtained. The range of percentages never varied more than 1.2 percent for any species.

Additional measurements were made to estimate errors in the following measurements: (a) filament length; (b) counts of secondary lamellae; (c) variations between left and right sides of gill sets; and (d) surface area measurements of secondary lamellae. Errors in measuring filament length using every twentieth filament were never greater than 3%, based on actual measurements of every filament from five randomly selected holobranchs. Errors in counts of secondary lamellae were never significant ($P > 0.05$), based upon counts of secondary lamellae along the lengths of center filaments from all holobranchs within a gill set from eight animals. Variations in filament length, secondary lamellae numbers, and surface areas between left and right gill sets were never more than 1%, based on comparisons of first holobranchs from five animals. Errors in surface area determinations were the largest source of error in this study, but were a function of the difficulties involved in removing entire lamellae, rather than from variations between gill arches. Extra care in secondary lamellae removal minimized this source of error (based on area determinations of secondary lamellae from center filaments of all holobranchs within a gill set from eight animals).

Results

A log/log plot of total gill surface area *versus* body weight is presented in Figure 1 for six of the seven species studied. No regression line is shown for the scalloped

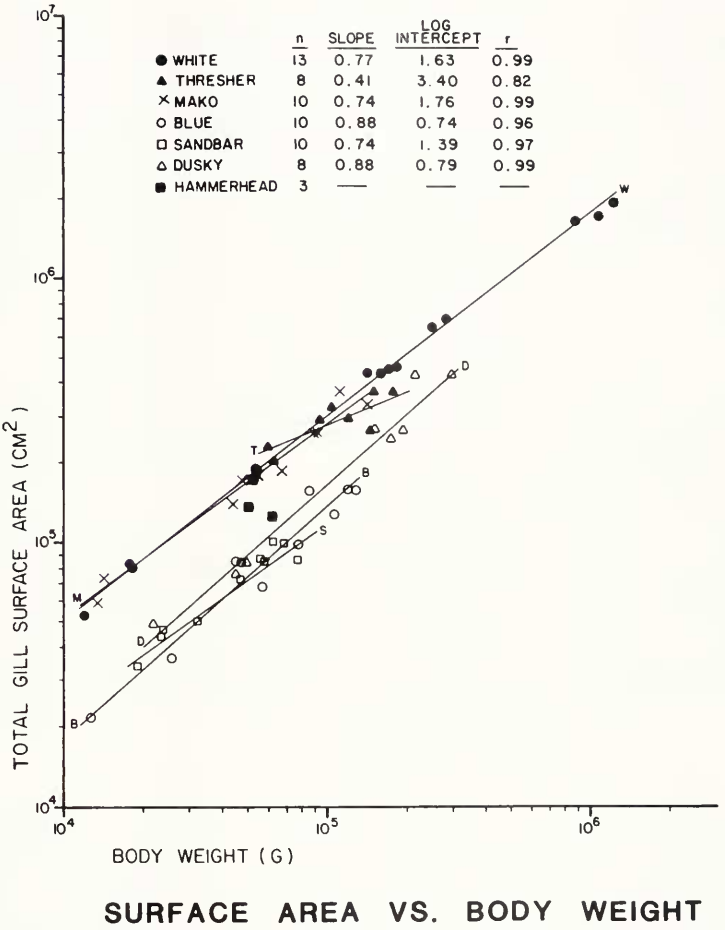


FIGURE 1. Linear regression lines demonstrating the relationships between total gill surface area (cm^2) and body weight (g) in six species of elasmobranchs.

hammerhead in Figures 1 through 4 due to the small number of animals available (three). The regression line for the common thresher, a species suspected to be endothermic (Carey, 1982), exhibits a radically different slope from the remaining five species, and results from the small range in body size of the specimens available for analysis. Differences in regression coefficients were too large to allow for statistical comparisons of all six species together. Only the shortfin mako and sandbar sharks were homogeneous with respect to regression coefficients [SS = 0.102 < SScrit .05 (5, 47)]. The shortfin makos exhibited larger total surface areas in comparison with sandbar sharks ($P < 0.05$).

Total surface areas in all six species were compared using the regression equations presented in Figure 1 to compute the TSA for each species at a common body size (Table I). At a body weight of 100 kg the $\hat{y}$ (estimated TSA based on the regression equation) for the white, mako, and thresher sharks are approximately twice the estimates for TSA obtained for the sandbar, blue, or dusky sharks.

In comparing total filament lengths (Fig. 2), only the great white and mako sharks

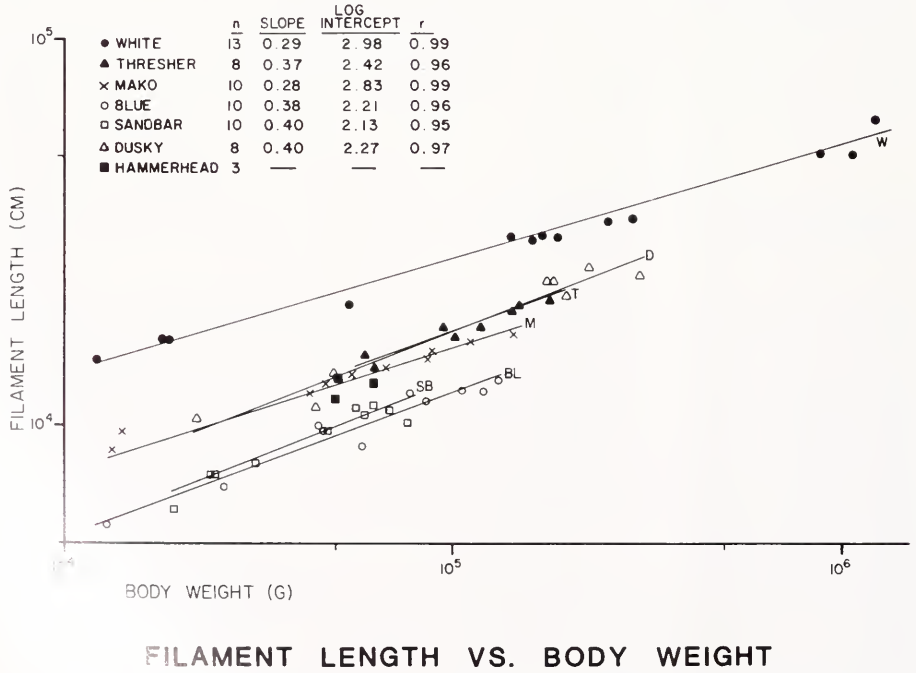
TABLE I

Gill dimensions at 100 kg weight (based upon regression equations shown in Figures 1–4)

Species	Total surface area (cm^2)	Total filament length (cm)	Weighted average number sec. lam. per mm	Weighted average sec. lam. area, 2 sides (mm^2)
Greak white shark	301,122	27,096	9.80	5.66
Common thresher shark	281,838	17,644	9.32	8.41
Atlantic shortfin mako shark	229,896	15,983	10.42	8.41
Dusky shark	154,882	17,758	10.89	4.23
Blue shark	138,038	12,367	9.54	5.76
Sandbar shark	123,027	13,051	10.44	4.60

had slopes similar enough to compare statistically [SS = 1.000; <SScrit 0.01 (5, 47)]. The great white shark exhibited significantly larger filament lengths than the mako at $P < 0.05$. From a qualitative view, total filament lengths in the great white shark are larger than those of any other species of shark (Table I).

However, the regression line of the white shark for the number of secondary lamellae per mm (Fig. 3) is not significantly above or below the regression lines of several of the ectothermic species (ANCOVA $P > 0.05$, combined with *a posteriori* STP [white shark, dusky shark SS = 0.921; <SScrit 0.05 (5, 47)] and sum of squares STP tests). At a body weight of 100 kg (Table I) the estimated values for the number of secondary lamellae per mm in the different species are similar ($P > 0.05$).



FILAMENT LENGTH VS. BODY WEIGHT

FIGURE 2. Linear regression lines demonstrating the relationships between total gill filament lengths (cm) and body weight (g) in six species of elasmobranchs.

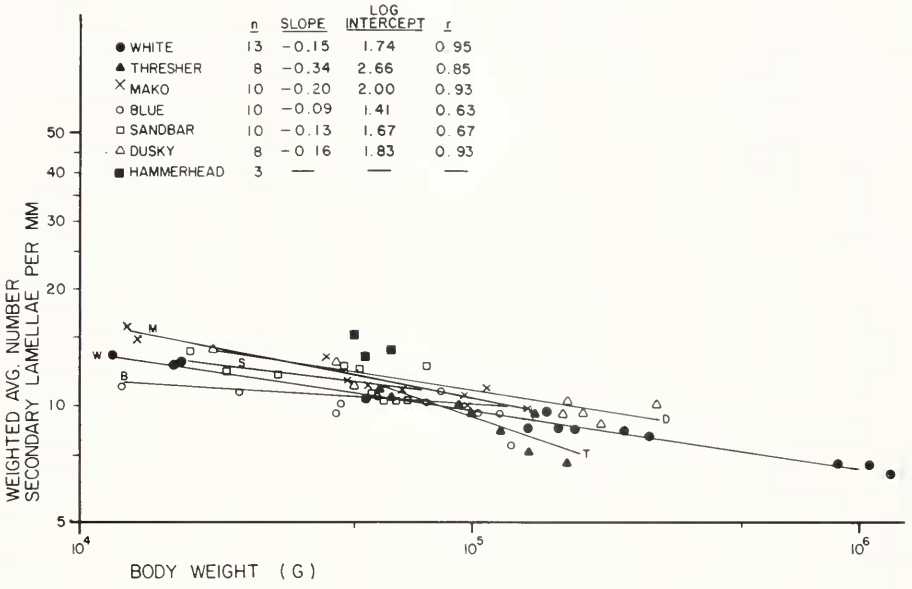


FIGURE 3. Linear regression lines demonstrating the relationships between the weighted average number of secondary lamellae per mm and body weight (g) in six species of elasmobranchs.

The regression line of the weighted average secondary lamellae area *versus* body weight (Fig. 4) for the white shark is not significantly different from the lines of one or more ectothermic species (ANCOVA $P > 0.05$, combined with *a posteriori* STP tests). At 100 kg (Table I) the estimated weighted average surface area of a secondary lamella is 5.66 mm^2 for a white shark, which is virtually indistinguishable from the estimated value of 5.76 mm^2 for a blue shark.

In contrast to the great white shark, our results indicate that the mako relies upon larger secondary lamellae to increase its total gill surface area (Fig. 4). A comparison of the regression coefficients for the mako and dusky sharks [SS = 0.028; <SScrit 0.05 (5, 47)] indicates that the mako possesses significantly larger secondary lamellae. Using $\hat{y}$ at 100 kg body weight (Table I) the shortfin mako has an average lamellae area of 8.41 mm^2, well above the estimated value for the next closest species.

The shortfin mako does not exhibit unusually large filament lengths (Table I and Fig. 2), nor a greater number of secondary lamellae per mm, (Table I, and Fig. 3) according to both statistical (ANCOVAs plus STP procedures) and qualitative methods of comparison.

The small size range and radically different regression coefficients for the thresher shark precludes meaningful statistical comparisons. Qualitative examinations of Table I and Figures 1 through 4 suggests that this species uses a similar method to that of the shortfin mako to increase its total surface area over the values estimated for the non-lamnid species.

The gill structure within the seven elasmobranchs studied is characterized by a high degree of interspecific conservativism. In addition to the similarities in lamellar spacing and size, no radically different secondary lamellar shapes were found between

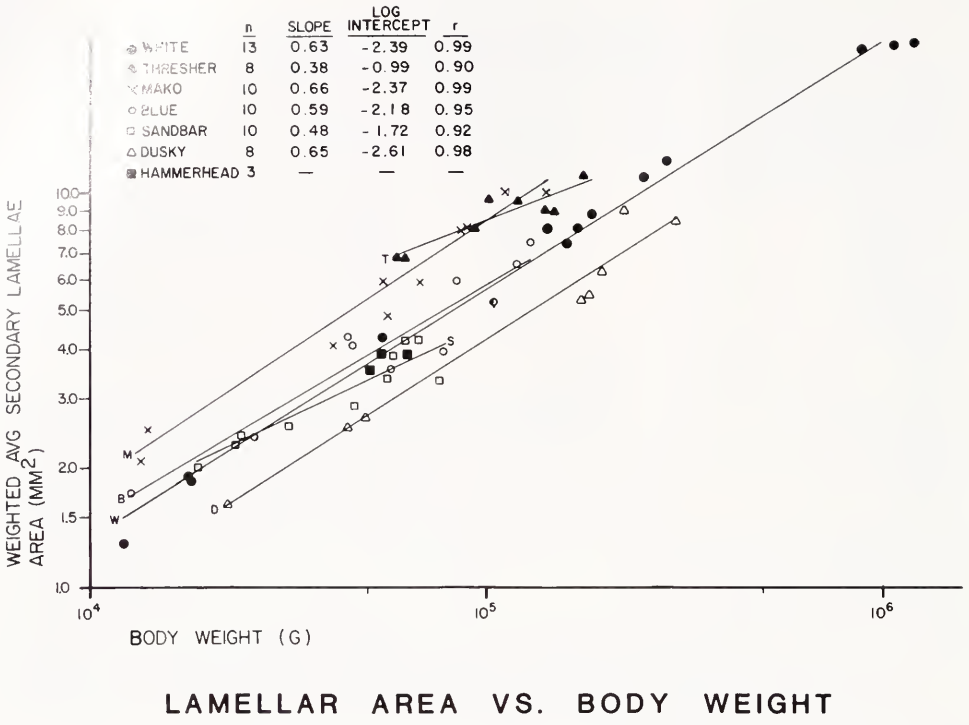


FIGURE 4. Linear regression lines demonstrating the relationships between the weighted average secondary lamellae area (mm^2) and body weight (g) in six species of elasmobranchs.

species at any given sampling location along a filament. Even the percentage of total filament length accounted for by the first holobranch varied less than 2% among all seven species.

No secondary lamellar fusion was noted in any individual gill examined. Filament fusion was occasionally observed in individuals of *all* species. The cause of filament fusion (developmental, parasitic, exposure to pollutants, *etc.*) is not obvious from macroscopic examinations.

DISCUSSION

From both a qualitative and quantitative viewpoint, the warm-bodied and presumed warm-bodied species of shark exhibit larger total gill surface areas than do active, pelagic, ectothermic species of shark. These results parallel those reported by Muir (1969), Muir and Hughes (1969), Randall (1970), and Hughes and Morgan (1973) for teleost fishes, in which warm-bodied tunas were found to possess greater surface areas than those of other species of ectothermic teleosts. Such large surface areas undoubtedly are necessary to facilitate adequate levels of oxygen uptake (Jones and Randall, 1978) to support the functionally endothermic condition (Carey and Teal, 1966; Stevens and Carey, 1981) and associated high metabolic rates (Brill *et al.*, 1978) found in these fish.

There are no studies on large elasmobranchs in the literature to facilitate comparisons to our data on gill surface areas. Hughes and Morgan (1973) list the total surface

TABLE II

Extrapolations of total gill surface areas per gram body weight in selected elasmobranch and teleost species

Species	Surface area per gram at 1 kg (cm^2/g)	Reference
Endotherms		
Skipjack tuna	18.40	Muir and Hughes, 1969
Yellowfin & bluefin tuna	14.38	Muir and Hughes, 1969
Atlantic shortfin mako	9.40	
Great white shark	8.72	
Ecotherms		
Sandbar shark	4.11	
Dogfish	3.70	Hughes and Morgan, 1973
Dusky shark	2.79	
Blue shark	2.39	
Smallmouth bass	1.96	Price, 1931, as presented by Muir and Hughes, 1969
Roach	1.29	Muir and Hughes, 1969

area of a 1 kg dogfish shark (*Squalus acanthias*) at 3.7 cm^2/g. This value, together with weight-specific values for tunas (Muir and Hughes, 1969), smallmouth bass (Price, 1931, using the regression line from Muir and Hughes, 1969), and roach (*Rutilus rutilus*) (Muir and Hughes, 1969) are presented in Table II, and are compared with values based on extrapolations down to 1 kg for all six of the species involved in this study. Values for the two warm-bodied shark species are substantially above those values for the ectothermic teleosts and elasmobranchs but do not equal those values found in tunas. Based upon the comparisons shown in Table II, plus information presented by Gray (1954), gill surface area values for the sandbar, blue, and dusky sharks fall within the range of most teleost fishes.

The way in which the endothermic lamnid sharks and tunas have successfully increased the surface areas of their gills as compared with non warm-bodied species differ. The tunas exhibit significantly larger total filament lengths per unit of body weight combined with increased numbers of secondary lamellae per mm to increase total surface area (Muir and Hughes, 1969). Individual secondary lamellae in tuna are smaller per unit body weight than in more sluggish teleosts (Muir and Hughes, 1969). The warm-bodied sharks do not exhibit increased numbers of secondary lamellae per mm nor smaller secondary lamellae per unit body weight. Only the great white shark exhibits larger total filament length. The mako and thresher do not.

Explanations for these differences between the lamnid sharks and the tunas are not obvious. It is possible that the extended gill septum in the elasmobranchs limits lamellar variability. It is clear that weight specific secondary lamellar numbers do not vary greatly among elasmobranch species. While secondary lamellar areas were significantly greater in the shortfin mako, this is the parameter in which the largest potential variability exists with respect to measurement error. Most teleost fishes have gill filaments free from connection with a septum for most of their lengths. The greater freedom allowed the teleost filaments may enhance the possibility for secondary lamellar enlargement and variation in spacing of lamellae on filaments.

Total gill filament numbers appear to be a species specific characteristic within the sharks we have observed. There are no trends of increases or decreases with body size. The percentage of the total number of filaments within each species accounted

for by the first holobranch remained relatively constant. These findings suggest that gill filament number could prove useful in certain species identifications, where other morphological examinations prove inconclusive.

The range of total filament numbers between the species is not large, in contrast to teleosts (Hughes and Morgan, 1973). The lowest estimate of filament count was found in a sandbar shark (1228 per side), the highest in a great white shark (1927 per side). There is no evidence to suggest that the endothermic species possess more filaments per se. Of the species we have examined, the ranking for total gill filament number is as follows (number ± SD per side): great white shark (1892 ± 27); dusky shark (1800 ± 49); common thresher shark (1483 ± 19); shortfin mako shark (1436 ± 32); scalloped hammerhead (1424 ± 25); blue shark (1304 ± 41); and sandbar shark (1249 ± 29). Hughes and Morgan (1973) reported total filament numbers of 749 in *Raja clavata* (0.5 kg) and 1000 in *Squalus acanthias* (1 kg). These data, in addition to our own, suggest that within the elasmobranchs at least, total filament number may be related to the maximum size limits of a species rather than to its ecology or physiology.

It is clear that the functionally endothermic species of shark exhibit larger total gill surface areas than do the non-endothermic forms. Because of the large size differences involved, direct comparisons between the warm-bodied sharks and the tunas are extremely difficult to make. From the limited data available (Table II), it appears that functionally endothermic sharks do not exhibit weight specific TSA values as high as those in tuna. To the extent that these morphological measurements provide insight into physiological performance levels, it may be that the lamnid sharks do not exhibit weight specific metabolic rates as high as those found in tuna and consequently cannot maintain as large a temperature gradient between the swimming musculature and the water as do tuna. The validity of these assumptions needs to be tested using both morphological and physiological information.

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